Systematics, Biogeography, and Ecology of Neartic Earthworms from Eastern, Central, Southern, and Southwestern United States

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I. Introduction

In the region of the United States east of the continental divide and near to or south of the southern limit of Wisconsinan glaciation, plus the coastal mountains of California south of Riverside and Santa Ana, there are native representatives of five (possibly six) earthworm families (Gates 1982, James 1990a). The five are Lumbricidae (*Bimastos*, *Eisenoides*), Megascolecidae (*Diplocardia*), Sparganophilidae (*Sparganophilus*), Komarekionidae (*Komarekiona*), and Lutodrilidae (*Lutodrilus*). The sixth is the Ocnerodrilidae, unidentified members

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of which have turned up in southern California stream beds (Wood and James 1993) and in North Carolina (James, unpub.). In this paper I will attempt to summarize the current state of knowledge of these groups with respect to their systematics, biogeography, ecology, and economic importance. The task may not be very lengthy, since little is known of the lives of these animals. Systematics and biogeography will be considered together. I will not go into details on analytical aspects of biogeography, but instead focus on ranges of the groups. Range maps are provided at the end of this chapter (Figures 1 to 7), but one must bear in mind that data on ranges of most species are sparse. After concluding the systematics and biogeography section with recommendations for future activity in these fields, I will summarize research to date on biodiversity conservation, ecology, and economic applications.

II. Survey of North American Native Earthworms

The organization (if not the content) of the above genera has been relatively stable for many years. One can imagine some reasons for this: the state of knowledge is complete and the relationships are so clear that there is no further reason to alter the system, or there has been so little work done on these worms that the current system's weaknesses have not been exposed. In some cases, the former is probably true, though one must add that new discoveries could change that. This is obviously true of the monotypic genera *Lutodrilus* and *Komarekiona*, for each of which a monotypic family has been defined. It may also be true of the monogeneric Sparganophilidae.

A. Lutodrilidae

Lutodrilus is known only from the section of Louisiana between Baton Rouge and Bogalusa, where it can be quite abundant in riparian areas and mud flats (McMahan 1976, Harman pers. comm.). I am not aware of any attempts to find earthworms in similar habitats along the Gulf Coastal Plain or in other New World mud flat sites to the south. *Lutodrilus* probably occurs in adjacent portions of Mississippi, but it is not clear if anyone has looked. McMahan (1976) reports accounts of unusual earthworm-like oligochaetes in the Mississippi valley and along the Gulf coast, but nothing resembling the animals has been collected and preserved for modern observation. Like fantastic reports of giant reptiles lurking in swamps of equatorial Africa, verification of the existence of other Lutodrilidae awaits a mud-loving and intrepid explorer.

The Lutodrilidae are related to the Almidae, Biwadrilidae, and Sparganophilidae, in order of decreasing similarity (Jamieson 1988). Jamieson's analysis does not support affinity of Lutodrilidae with the lumbricoid families Lumbricidae, Glossoscolecidae, Hormogastridae, Komarekionidae, etc., as was thought to be the case by McMahan (1976). The Lutodrilidae and families similar to it are

aquatic or limicolus (mud-inhabiting). The Almidae occur in Europe, Africa, and Asia, with one record in Central America, the Biwadrilidae are unique to Japan, and the Sparganophilidae are North and Central American. Because the ancestors of opisthoporous oligochaetes were probably aquatic or semi-aquatic, it should not be surprising to find a globally-distributed higher taxon of aquatic to limicolous families (cf. Jamieson 1988).

B. Sparganophilidae

The Sparganophilidae are known from the entire geographic area covered in this chapter, except for the desert Southwest. However, it is probable that no one has ever looked for them there. The only genus, *Sparganophilus*, contains 13 species, a key to which is in Reynolds (1980). Two species are known from northern California and Oregon, and the rest from central, eastern, and southern states, plus the Canadian province of Ontario (detailed distribution data are in Reynolds 1975, 1977a, b, 1980). *Sparganophilus eiseni* has colonized aquatic and semi-aquatic habitats well to the north of the glacial boundaries (Smith and Green 1916, Reynolds 1977a). They may be found as lake benthos, in wet soils of stream banks or in saturated sediments along the edges of streams. New southern California records of an as yet undetermined *Sparganophilus* are in Wood and James (1993). The Sparganophilidae are most closely related to the Biwadrilidae, Lutodrilidae, and Almidae (Jamieson 1988), though classically they have been placed in or near the Glossoscolecidae (Michaelsen 1900, Stephenson 1930).

Species delineations within *Sparganophilus* are fairly clear, though the differences are often subtle, and many species descriptions are based on examination of very few specimens. The range of the most well-known species, *S. eiseni*, encompasses the ranges of its congeners except those of the Pacific region. In this case, one must be careful to determine if the range of morphological variation within *S. eiseni* is so narrow as to exclude the other species of the genus. Future research on *Sparganophilus* should focus on expanding collections of known species, searching unexplored areas, and otherwise clarifying the relationships among the various species.

C. Komarekionidae

The range of *Komarekiona eatoni* is in deciduous forests of the eastern United States, from southern Pennsylvania south to North Carolina and Tennessee, and west into southern Indiana and Illinois (Gates 1974, 1982, Dotson and Kalisz 1989, James unpub.) However, Gates did not consider the Illinois and Indiana records to be in the natural range of the species. Though Gates (1974) created the Komarekionidae for this species, Sims (1980) has argued that it belongs in the Ailoscolecidae. Jamieson (1988) supports the family Komarekionidae, his

analysis showing it as sharing a common ancestor with all other Lumbricoidea. Therefore, *Komarekiona* is of some systematic interest in determining the relationships within the superfamily and between the Lumbricoidea and other superfamilies.

The two remaining families with members clearly indigenous to temperate North America are the Lumbricidae and the Megascolecidae. Both are represented by many species and both are widely distributed in terrestrial habitats.

D. Lumbricidae

Indigenous North American Lumbricidae fall into two genera, *Eisenoides* and *Bimastos* [see Schwert (1990) for a key]. The former is exclusively Nearctic and contains only two species so far. The latter is more diverse and has been assigned some species known only from Europe (Gates 1972a). *Eisenoides carolinensis* is found in mesic deciduous forested areas of the eastern United States, from the southern half of Pennsylvania to the Carolinas (Gates 1972b). It can be quite abundant locally. *Eisenoides lonnbergi* has approximately the same range, but extends farther north nearly to Lake Ontario. It inhabits wet areas, such as stream banks or stream beds, acid bogs, chronically damp soils and calcareous fens (pH range 4–7.8!). Generally it is found within forested areas, including coniferous forests of hemlock and white pine. It is probably the most northerly-distributed native earthworm of eastern North America, except for *S. eiseni*.

The genus *Bimastos* is generally found throughout the parts of eastern North America not glaciated in the Wisconsinan period and as far west as Kansas. It is also found in scattered locations in Michigan (Murchie 1956) and other areas slightly to the north of the glacial maxima. Most species are confined to forests where, with one exception (*B. longicinctus*), they live under the bark of decaying logs or in accumulations of organic matter such as leaf packs at the bases of slopes or near small drainages. *B. tumidus* has been observed to colonize rotting bales of straw in southeast Iowa and to be transported when the straw is moved from one location to another. Some species have been transported to other continents (Smith 1917, Gates 1972a).

Bimastos longicinctus also inhabits forested areas and rarely grasslands, but lives in the mineral soil rather than in highly organic media. *B. welchi* lives in tallgrass prairie of Missouri and Kansas, and has been collected from a nearly barren rocky slope on an otherwise forested hillside in west central Missouri. It is abundant in the Flint Hills of Kansas.

Currently, ten species of *Bimastos* are recognized. Other new species have recently turned up in North Carolina and the northern Appalachians (James, unpub., Schwert, pers. comm.). Ignoring for now the relationships of the North American *Bimastos* to European congeners, there is little dispute over the systematics of the group. Gates (1982) commented that *Bimastos* is composed

of "parthenogenetic morphs, some nine or more of which have been regarded as species." In relation to this important evolutionary/systematic issue (can clonal organisms be regarded as species?), there should be an examination of the evidence for the alleged near-universality of parthenogenesis in *Bimastos*. I have collected numerous *B. welchi* bearing spermatophores. In much less extensive collecting than what took place in Kansas, I have found spermatophores on many other *Bimastos* species. I suggest that experimental and genetic approaches to determining the mode of reproduction in these and other reputedly parthenogenetic earthworms will be more convincing than noting the lack of spermathecae.

Other substantive concerns about *Bimastos* are raised in the unpublished notes of Gates. It appeared to him that there are forms intermediate between certain species, and that some of the key characters used in identification may be unreliable. His work was heading in the direction of locating reliable internal characters for defining species and identification of them.

E. Megascolecidae

The sixth earthworm genus indigenous to the geographic area considered here is *Diplocardia*. I am following the classification proposed by Jamieson (1971a, b) and placing it in the subfamily Acanthodrilinae of the Megascolecidae. The Acanthodrilinae as defined by Jamieson are not necessarily equivalent to the Acanthodrilidae of other authors, so one should check before assuming that a genus said to belong to the Acanthodrilidae belongs to the Acanthodrilinae.

The range of *Diplocardia* extends from the southern half of Pennsylvania west through parts of Ohio, extreme southern Michigan, the southern halves of Indiana, Illinois, Iowa, and Nebraska, and south to Florida, the Gulf Coast, and west central Texas, plus records from Jeff Davis County in southwest Texas (Gates 1977). Then there is a gap in the known distribution, except for a few sporadic records from feedlots in New Mexico and Arizona (Gates 1967b) until California south of the Los Angeles basin. In that region some species live in native grassland remnants at middle and high elevations (Wood and James 1993, James 1994a). These new species are related to *D. keyesi*, known only from northern Baja California, Mexico (Eisen 1896). There are other *Diplocardia* from Mexico, but these will be considered in Chapter 4.

Diplocardia is closely related to the other acanthodriline genera *Notiodrilus* and *Diplotrema*, in that all have avesiculate holonephridia and the acanthodriline arrangement of male genitalia. *Diplocardia* differs in having a gizzard extending through two segments rather than one. The *Diplocardia* gizzard appears as one unit with little or no dividing line at the insertion of the septum 5/6, which septum is thin and membranous. This is in contrast to the obvious thinning of the gizzard wall and constriction at the septa that occur in *Zapotecia* and an undescribed species of a new Mexican genus related to *Zapotecia* (James 1994b). These distinct modes of gizzard multiplication or enlargement indicate that a common ancestor of *Diplocardia* and *Zapotecia* is probably monogiceriate,

Table 1. The currently recognized names of North American earthworms from the area east of the Rocky Mountains.

Komarekionidae
Komarekiona eatoni Gates 1974
Lumbricidae
Bimastos beddardi Mich. 1894
B. ducis Stephenson 1933
B. gieseleri Ude 1895
B. heimburgeri Smith 1928
B. longicinctus Smith and Gittins 1915
B. palustris Moore 1895
B. parvus Eisen 1874
B. tumidus Eisen 1874
B. welchi Smith 1917
B. zeteki Smith and Gittins 1915
Eisenoides carolinensis
E. lonnbergi
Lutodrilidae
Lutodrilus multivesiculatus McMahan 1976
Sparganophilidae
Sparganophilus eiseni Smith 1980
S. gatesi Reynolds 1980
S. helenae Reynolds 1980
S. komareki Reynolds 1980
S. kristinae Reynolds 1980
S. meansi Reynolds 1980
S. pearsi Reynolds 1975
S. smithi Eisen 1896
S. sonomae Eisen 1896
S. tennesseensis Reynolds 1977
S. wilmae Reynolds 1980
Megascolecidae
Diplocardia: with calciferous lamellae
D. alabamana Gates 1977
D. alba Gates 1943
D. bivesiculata Murchie 1961
D. eiseni Mich. 1894
D. farmvillensis Gates 1977
D. floridana Smith 1924
D. gatesi Murchie 1965
D. komareki Gates 1977
D. macdowelli Murchi 1967
D. michaelseni Eisen 1899
D. minima Gates 1977
D. mississippiensis Smith 1924
D. pettibonae Gates 1977
D. udei Gates 1955
D. vaili Gates 1977
D. varivesicula Murchie 1966
Diplocardia with spermathecae in segment vii:
D. biprostatica Gates 1977
D. communis Garmann 1888
D. caroliniana Eisen 1899
D. fusca Gates 1943
D. glabra Gates 1967
D. hulberti James 1988
D. longa Moore 1905
D. meansi Gates 1977
D. nova Gates 1977
D. ornata Gates 1943
D. sandersi Gates 1955
D. singularis Ude 1893
D. sylvicola Gates 1977
Other species:
D. bitheca Gates 1977
D. conoyeri Murchie 1961
D. fuscula Gates 1968
D. gracilis Gates 1943
D. invecta Gates 1955
D. kansensis James 1990
D. keyesi Eisen 1896
D. longiseta Murchie 1963
D. riparia Smith 1895
D. rugosa James 1988
D. smithii MacNab and McKey-Fender 1955
D. texensis Smith 1924
D. verrucosa Ude 1895

as opposed to the scheme proposed in Pickford (1937).

The other members of the Acanthodrilinae occur in Mexico and Central America, Chile, Argentina, South Africa, New Zealand, Australia, Madagascar, and various subantarctic islands (Pickford 1937, Michaelsen 1900, Lee 1959, Jamieson 1971a, b). This distribution is essentially Gondwanan, with an extension into North America.

Eisen (1896, 1900) proposed several subgenera of *Diplocardia*, none of which has been used since. The criterion was location of the male pores, which is quite variable among species known then and is more variable among species known now. The usual male pore location is xix, unlike most Acanthodrilinae in which it is in xviii. In Gates (1977) the species are arranged in three groups, those with calciferous glands, those with three pairs of spermathecae, and "other" species. Of these, only the first one is probably a natural grouping. However, in Gates (1977), *D. koebeli* is erroneously assumed to have calciferous glands. The species with calciferous glands are found from Pennsylvania south to Florida and west along the Gulf Coast states into Texas. The calciferous glands are of one basic type, differing in their degree of development and in their segmental location. There is little reason to suspect that calciferous glands arose independently in more than one lineage of *Diplocardia*.

My preliminary analyses suggest that a second natural group would be those species with spermathecae in segment vii, which includes the species with three pairs of spermathecae and two others with one and two pairs. This group is found throughout the range of the genus, except the Californian and Mexican portions. The bulk of the species are southern and central.

The remainder of the *Diplocardia* consists of species with two pairs of spermathecae and no calciferous glands, but is diverse with respect to male pore location and several other characters such as segment of intestinal origin and configuration of the spermathecae. Most of these species are from the central states and south into Texas. The species with posterior displacements of the male pores are mostly from the western portion of this zone and from California/Baja California.

While there are no absolute criteria for splitting or lumping of genera, *Diplocardia* now contains a greater diversity of character states than most authors seem to tolerate in other genera. For example, few other genera in the Megascolecidae include species with and without calciferous glands. A great deal of the generic definitions in the Glossoscolecidae depend on numbers and kinds of calciferous glands, and absence would be a cause for elevation to generic rank in that family. Male pores range from xviii to xxii within the "remainder" category of *Diplocardia*, a diversity that may be unparalleled in any other earthworm genus. If *Diplocardia* has survived intact this long, it is probably because the species "look like *Diplocardia*" and no one has wanted to break up a natural-seeming group. The time may be coming, because many new species in all sections of the genus have been collected (James, unpub. data).

There are some species or species groups for which the current system of classification is unclear. One group is *D. singularis* and *D. caroliniana* and their

subspecies. The distinguishing characteristics are few, their variability considerable, and at least one subspecies, *D. singularis fluviatilis* may merit species rank. It inhabits mudflats of the Illinois River, whereas other *D. singularis* are found in dryland soils. It is possible that some subspecies, or some of the other variation, is associated with parthenogenesis, as appears to be true of *D. s. egglestoni* (Murchie 1958).

Another trouble spot is developing with *D. communis*, its subspecies *wolcotti*, and *D. nova*. One of the characters used to distinguish among them is the extent of doubling of the dorsal blood vessel. Unfortunately this character is highly variable in specimens recently collected in Iowa and Missouri. It may be necessary to rethink the species definitions. More useful characters may exist, but have not been fully explored or incorporated into keys.

Apart from these there are hints of geographic variation within worms that key to *D. verrucosa*, a very distinctive variant of *D. alba* given subspecific rank as *gravida* (Gates 1977), and numerous morphs and variants mentioned in Gates (1977). This amounts to saying that there is quite a bit of work yet to be done. Considering that most of the range of the genus has not been surveyed except in a very spotty fashion, this is not surprising.

From the practical point of view, we need to make progress in making it possible for everyone working on North American earthworms to identify their species. Doing taxonomic work may be fun for some, but many people have only one desire: to get a name for the specimen. Fender and McKey-Fender (1990), James (1990a), and Schwert (1990) made some headway, but there are some simple steps I believe would be very effective. The first would be periodic publication or distribution of updated keys. The keys should be accompanied by illustrations and a brief diagnosis of each species. Second, a computerized identification system/database should be kept and updated annually or as necessary. The software for this exists now and the whole package could be distributed over a computer network, such as INTERNET. Finally, there needs to be more support for the taxonomic work that could be done on material presently in collections and for surveying of the little-explored areas of North America.

III. Biodiversity and Conservation Concerns

What do we mean by biodiversity? Among ecologists it is commonly understood as having something to do with species richness and evenness. Recently people began using it in a broader sense as "something that ought to be saved." Some of the important elements of a program to preserve biotic diversity are (1) awareness of the existence of the taxa to be preserved, (2) knowledge of the requirements for their preservation, (3) knowledge of present and future threats to the persistence of the taxa, and (4) social and political weight behind the programs to accomplish preservation. With reference to the earthworm genera discussed here, there are serious deficiencies in the first three, and it may be

difficult to achieve the fourth at all. We simply do not know how many species of earthworms exist in North America and we do not know the range of any species with any confidence.

For some species it is possible to make educated guesses at the requirements for preservation. For example, most *Bimastos* species will be satisfied with a tract of forest with fallen trees in various stages of decomposition. From collection records we can glean the typical habitat conditions, but these do not necessarily represent minimum requirements. Considering the potential influences of exotic species of earthworms on the natives in their natural habitats, even habitat protection may fail (Dotson and Kalisz 1989, Kalisz and Dotson 1989). Nevertheless, preservation of ecosystems will reserve habitat for many cuteness-disadvantaged organisms, and probably is the best bet.

Threats to an earthworm species generally come from habitat destruction and invasion of exotics, singly or in combination (Smith 1928, Lee 1961, Stebbings 1962, Ljungstrom 1972). To date there are no experimental data on competition between native and introduced species from any system. This should be a top research priority. I have attempted the experiment twice without success. In both cases there was difficulty getting an area free of exotic species in which to install the experiment. Worm-free zones can be created in the field, but only at the cost of mass use of poisons or use of sites so severely disturbed that the generality of any results could be questionable. One alternative is to seek sites in naturally worm-free habitat in glaciated regions. These are not difficult to find, but are generally quite north of the ranges of the native species. That may introduce other factors irrelevant to the question about the outcome of a competitive interaction within the natural range of the native species.

IV. Ecology of North American Species

A. Population Studies

Very little is known of the population dynamics or demography of North American earthworms. Murchie (1960) obtained information on the natural history of *B. zeteki* and Vail (1972) on natural history and reproduction in *D. mississippiensis*. James (1988b) contains data on population dynamics in relation to controlled burning. Populations of *Diplocardia smithii* and *D. verrucosa* had positive responses to fire in tallgrass prairie, while exotic Lumbricidae declined. The differences are probably related to different temperature tolerances, the native species being able to remain active at higher soil temperatures. Data gathered during the burning [illegible] projects were used to analyze seasonal changes in size-class distributions and response to dung pats in several species of *Diplocardia* and *Bimastos welchi* (James 1992a, b, *B. welchi* was erroneously identified as *Octolasion cyaneum*). From the former it was possible to conclude that different species of *Diplocardia* reproduced in different seasons, and that *B. welchi* has a very short early spring breeding period. Further

information on seasonality of reproduction can laboriously be extracted from collection records, but there is no other research specifically on this subject.

James and Cunningham (1989) compared gut contents of several species of *Diplocardia*, *B. welchi* (again incorrectly identified as *O. cyaneum*) and *Aporrectodea turgida* and related the results to predictions of ecological niche based on gut morphology (cf. Lee 1959). There were good relationships between the data and predictions, but the relationships were most clear within family. Some *Diplocardia*, particularly *D. kansensis*, clearly fed on surface litter, while others fed in the soil. *Bimastos welchi* fed deepest in the soil of all native species, in stark contrast to the feeding behavior of its forest congeners.

There are some studies relating earthworm species populations to habitat, microsite, and/or soil influences (Murchie 1956, James 1988, Dotson and Kalisz 1989, Boettcher and Kalisz 1991, Wood and James 1993). Most of these describe naturally-occurring situations and consequently do not definitively test hypotheses about causation. They do not answer questions about why the worms do not live in other places or about factors controlling population sizes. This should be taken as suggestion, not as criticism. It really makes little sense to charge into sophisticated experimental design without a basis for the elements of the design. These studies provide good starting points. Just as plant ecology made a transition from largely descriptive work to extensive experimentation, we should look towards the same.

B. Community Ecology and Earthworms

There has been no published research on the relationships among North American native earthworms and other biota, such as soil fauna. An example of a potential research program would be to investigate the effects of earthworm activity on soil arthropods. One could hypothesize that pore size distribution changes could affect the population sizes or species composition of the arthropods. In another example, earthworm alterations of litter decomposition rates may dramatically alter the soil/litter faunal community. It is possible that there may be further effects on other groups of organisms, such as fungi, bacteria, and plants. However, there has been no research in these areas.

C. Agricultural and Other Economic Applications of North American Earthworms

The majority of research (what little there is so far) on earthworm ecology in pasture and arable lands in North America has dealt with European Lumbricidae. An exception is Teotia et al. (1950), in which a worm identified as *Diplocardia riparia* was present in cropland. The authors noted some differences in the stability of casts produced by native and introduced species. Gates (1967a, 1968) obtained specimens of *D. glabra* and *D. fusca* from Louisiana agricultural

fields. Parmelee et al. (1990) and Hendrix et al. (1992) reported the presence of *D. caroliniana* in no-tillage agricultural fields and *Diplocardia* spp. in pastures on the Georgia piedmont. *Diplocardia* may be more important in croplands of southern areas because exotic Lumbricidae may experience high temperature limitation. On the other hand, there may be *Amynthas* species (Megascolecidae; from Asia) capable of colonizing these same areas.

Bimastos tumidus can become established in compost piles. I have observed it to multiply rapidly in old straw and spoiled hay as well, and to spread from one pile to another. This species has the potential to be useful in organic waste management or composting. This has not been rigorously researched, but it seems that it does well at medium C/N ratios (cool temperatures of decomposition), compared to *Eisenia foetida*. In the future it may be possible to propagate *B. tumidus* for acceleration of decomposition without raising the problems associated with introducing an exotic species. Another advantage is its apparent ability to survive ordinary soil conditions in the cold continental climate (USDA hardiness zone 5) of Iowa. Thus once established in an area, it would persist without periodic expensive reintroductions.

This is one example for which some preliminary observations are available. With dozens more native species from which to choose, it is possible that more will turn out to have economic uses.

Several species of *Diplocardia* are currently collected commercially for bait from natural populations in Kansas, Missouri, and Florida. Still others are used on a smaller scale, principally the larger species (e.g., *D. mississippiensis* and *D. floridana*) of southern states. Worm gathering is regulated in the Apalachicola National Forest of Florida, where the industry is of some importance. In Kansas and Missouri there is no regulation to date, so it may not be easy to determine the economic importance of *D. riparia*, the target species (sold as river worms). Fishermen in Kansas favor river worms for summer fishing because they do not require refrigeration (vs. *Lumbricus terrestris*) and remain lively longer in warm summer waters.

V. Research Imperatives

It is obvious from the foregoing discussion that deficiencies exist in our knowledge of North American native earthworms. This section identifies specific research directions aimed at overcoming these deficiencies.

A. Biological Survey and Inventory

Much of the continental United States has not been systematically surveyed for native earthworms. Basic information on the presence and abundance, and habitat relationships of species in all five families are needed across these poorly

studied regions. In particular, the Gulf Coast drainage systems may yield new species of *Diplocardia* and possibly of *Lutodrilus*. Work is also needed on the Sparganophilidae, including expansion of collections of known species and surveys of unexplored areas for new species.

B. Systematics and Evolutionary Issues

A number of unresolved questions need further research:

- Is *Komarekiona eatoni* best placed within Ailoscolecidae? What is the relationship of Komarekionidae to other families within the Lumbricoidea?
- Is parthenogenesis nearly universal in *Bimastos*? The occurrence of spermatophores in many species suggests otherwise. Experimental and genetic studies are needed to determine mode of reproduction. There also is need to continue the unfinished work of Gates in locating reliable internal characteristics for defining and identifying *Bimastos* species.
- Is *Diplocardia* a "good" genus? Three distinct natural groupings occur, based on morphology and partly on biogeography. The diversity of character states is greater than in most genera within the Megascolecidae and related families, and is increasing as new species are found. Furthermore, classifications are unclear for several species and subspecies (e.g., *D. singularis*, *D. caroliniana*, *D. communis*, and *D. verrucosa*). A thorough analysis and reevaluation of the genus is needed.

To better serve the needs of the research community, taxonomic keys to native and exotic species need to be updated periodically, with improved illustrations and brief diagnoses. Computerized identification systems should be distributed on computer networks for wider accessibility and easier updating. Finally, more support is greatly needed for taxonomic work, both on existing collections and on new collections from unsurveyed areas of North America.

C. Biodiversity and Conservation

There are serious deficiencies in our knowledge of abundance and distribution of native earthworm species, their habitat requirements, and present and future threats to their existence throughout North America. Further, it is not clear that there is sufficient social or political interest to foster conservation of earthworm biodiversity. Because the greatest threats to earthworm species are habitat alteration and invasion of exotics, current efforts toward management and preservation of whole ecosystems should be promoted, and, as a top priority, experimental research is needed to investigate competitive interactions between native and exotic earthworm species. The importance of the latter is almost completely unknown.

D. Ecology of North American Species

- Little is known about the life history (e.g., population dynamics and demography) of native earthworms. Studies are needed especially on seasonality of reproduction and feeding ecology (i.e., niche characteristics). Experimental work on relationships between populations and habitat, microsite, and soil influences would reveal controls on distribution and abundance.
- Interactions between native earthworms and other biota are poorly known. Studies of effects of native species on plants, microbes, and other soil fauna would be useful contributions in this area, and would aid our understanding of the role of native earthworms in ecosystem processes.

E. Applied Ecology and Economic Considerations

- Little attention had been paid to native earthworm species in agricultural soils in North American. *Diplocardia* species may be important in the southern U.S. because of their tolerance of higher temperatures compared to introduced lumbricids which dominate in agricultural areas of the midwest, and which have been shown to significantly influence soil processes there.
- Further research also may show an important role for species of *Bimastos* (e.g., *B. tumidus*) in vermicomposting, which is increasing in use in the U.S.
- Finally, "cottage" fish-bait industries based on native earthworms exist in several states in the U.S. Mostly, these rely on harvesting worms in forests but research on techniques for cultivating these species could increase their production and reduce the demand for exploitation in natural ecosystems.

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Figure 1. The approximate North American distribution of *Komarekiona eatoni* and *Lutodrilus multivesiculatus*.

Figure 2. The approximate North American distribution of *Sparganophilus* spp.

Figure 3. The approximate North American distribution of *Bimastos* spp.

Figure 4. The approximate North American distribution of *Eisenoides* spp.

Figure 5. The approximate North American distribution of *Diplocardia* spp. with calciferous lamellae.

Figure 6. The approximate North American distribution of *Diplocardia* spp. with spermathacae in segment vii.

Figure 7. The approximate North American distribution of miscellaneous *Diplocardia* spp.